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STUDIES FOR STUDENTS.

THE DEVELOPMENT AND GEOLOGICAL RELATIONS OF THE VERTEBRATES.

II. AMPHIBIA.

THE *Amphibia* may be described as forms that live a portion of their lives, at least, in the water or in a condition fitted for an aquatic existence; the latter statement is necessary from the fact that some forms never live in the water, but develop external gills such as are found in the forms which do pass the larval stage as aquatic forms. All amphibians pass through a metamorphosis in which the external gills of the immature forms are lost and lungs developed. The skull presents some peculiarities; the whole base of the cranial region is covered by a large presphenoid bone that extends far forward as well as backward. In the more highly developed types of the vertebrates this bone occupies a minor position anterior to the basioccipital. In many of the more primitive forms of the amphibians the bones of the cranial region are largely cartilaginous; the extremities of the long bones of the limbs are without the epiphyses, or separate ossifications, that are found in the mammals, and the ribs are attached each to a vertebra instead of intervertebrally as in the higher forms.

That the *Amphibia* were derived from the *Pisces* is without question, but from what branch of the piscine stem they were developed has been the subject of much discussion. For a long time they were supposed to be derived from the *Dipnoans*, and from forms that were very close to the existing genera of the order. This idea is still supported by Haeckel (*Systematische Phylogenie der Wirbelthiere*; Berlin, 1895). In discussing the question, Baur said (The Stegocephali: a phylogenetic study;

Anatomischer Anzeiger, Band XI, Nr. 22, 1896, p. 659) "That the *Stegocephali* (the most primitive of the amphibia) did take their origin from a group of fishes is evident. The question to examine is: Which was this group?"

"In the Devonian preceding the Carboniferous, where the *Stegocephali* first appear, we have the following groups of fishes: The *Elasmobranchii*—including the *Holocephali*—*Ostracodermi*, *Dipnoi*, *Crossopterygii* and *Chondrostei* (this last group corresponds to the *Actinopterygii* of the present studies). The *Elasmobranchii* have no dermal ossifications in the skull, they are therefore out of the question; the *Ostracodermi* have, of course, nothing to do with the *Stegocephali;* we also can exclude the *Chondrostei* represented by *Cheirolepsis*. Only the *Dipnoi* and the *Crossopterygii* remain.

The dentition of the *Dipnoi* is already so much specialized in the Devonian, that it is impossible to derive the *Stegocephali* from them. We have now to consider the *Crossopterygians*. The *Crossopterygii* were established by Huxley, in 1861, to contain the living *Polypteridæ* of Africa and the extinct *Holoptychidæ*, *Rhizodontidæ*, and *Osteolepidæ*, having lobate paired fins with an endoskeletal axis, more or less fringed with dermal rays. The *Crossopterygii* are the most typical fishes of the Devonian. There is no difficulty in homologizing the premaxillaries, nasals, frontals, parietals, prefrontals, and postfrontals in the *Crossopterygii* and the *Stegocephali*." Here the author proceeds to prove from the course of the grooves upon the skulls of certain of the more primitive of the fishes and the amphibians, which mark the course of the sensory tracts of nerves in the living form, the homology of the skull bones of the two groups and the close connection that exists between them.

In a further discussion of the homology of the ribs he concludes that the "ribs of the oldest *Batrachia*, the *Stegocephali*, are not homologous with the ribs of the *Dipnoi*; therefore the *Dipnoi* cannot be the ancestors of the *Stegocephali*," and "the *Batrachia* must have developed from the *Crossopterygii*."

The *Amphibia* may be classified as follows:

Class, AMPHIBIA.
    Order, *Labyrinthodontia.*
        Suborder, *Branchiosauria.*
            Microsauria.
            Aistopoda.
            Labyrinthodonta vera.
                a, *Embolerimi.*
                b, *Rachitomi.*
                c, *Labyrinthodonti.*
    Order, *Coecilia.*
        Caudata (*Urodela*).
        Suborder, *Salamandrina.*
            Icthyoidea.
    Order, *Ecaudata* (*Anura*).
        Suborder, *Arcifera.*
            Firmisterna.
            Aglossa.

It is with the first of these orders that the student of palæontology is the most concerned, as they were the predominant forms of life during the Carboniferous time and even during the first part of the Mesozoic. The other orders did not assume any importance before the beginning of the Tertiary, and only one of them, the *Caudata*, appeared as early as the Cretaceous.

The earliest trace of amphibians is found in the Devonian rocks of Warren county, in Pennsylvania, and consists of tracks of some large labyrinthodont that Marsh has called *Thinopus antiquus* (*Am. Jour. Sci.*, 1896). No other trace of the *Amphibia* has been found in rocks earlier than the Carboniferous, but with the appearance of that time a large number of forms were developed that in the variety of their forms and the degree of their specializations rivaled the development of the reptiles of later times. To this large group of semi-aquatic forms Huxley gave the name *Labyrinthodonta* in 1863; five years later Cope gave the name *Stegocephali* to the same group. The latter name is used the most commonly in this country.

In external appearance the *Labyrinthodontia* were very similar to the existing tailed amphibians, the body was long in some cases and in others more stout and heavier; the skin was naked, but in most cases, on the ventral surface, at least, protected by the development of small dermal ossicles of bone; the legs were in most of the forms rather short and weak, and in some cases were entirely atrophied as in the recent snakes; the bones of the more primitive forms were quite largely cartilaginous, the carpus and the tarsus of some forms being almost entirely so, and even the long bones of the limbs and the bones of the skull were incompletely ossified; the skull was completely roofed over by dermal bones developed in the skin of the head, leaving only five openings in the skull, the two nostrils, the orbits, and the pineal foramen, the last a single opening on the upper surface of the skull. The teeth of most of the forms, and of the more highly developed forms of the Trias especially, are notable for the peculiar infolding of the enamel, giving the internal structure of the tooth a most complicated appearance.

The structure of the spinal column in the various forms is of especial interest, as it parallels in the first stages the history of the spinal column of the fishes and takes the process a few steps farther. In all of the *Labyrinthodontia* the notochord is to a greater or less extent persistent. In the simplest of the *Amphibia* the chord is very large and the vertebræ are represented by small plates arranged in pairs on the upper and lower surface of the chord; to these plates are attached the spinuous processes and the hæmal arches that protect respectively the spinal chord and the nutrient arteries (in the amphibians the hæmal arches are complete only in the caudal region). The next stage in the development of the column is the union of the plates, on the upper and the lower side of the chord, to form a complete cylinder that incloses the chord. The cylinder is of equal bore throughout and does not constrict the chord or tend to divide it up into segments. These two conditions are found only in the most simple of the amphibians and are well illustrated in the immature and mature forms of the *Branchiosauria* (Fig. 1, *A*). The next step is the thickening of the walls of the middle portion of the cylinders that surround the notochord so that the bore is very small at the center, while at the anterior and the posterior ends the bore is still full size; this tends to divide the notochord at the middle of each vertebra and to leave intervertebral segments. This condition of the vertebræ, with deep cups at each end, is called "biconcave." It is the same condition that is found in the primitive reptiles, and the closing of the notochordal canal and the filling up of either the anterior or the posterior cups of the vertebra would complete the development of the highest type of the reptilian vertebra. (Fig. 1, *B.*)

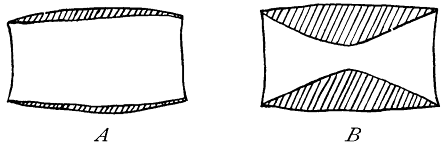

FIG. 1.—*A* Section of Branchiosaurian vertebræ showing size of notochordal canal; *B* Section of microsaurian vertebræ showing contraction of notochordal canal.

Another type of vertebræ that was developed by the amphibians seems to be somewhat more primitive than the last described, and also to be somewhat off the line of direct development. There were four distinct pieces, an upper, that supported the spinuous process, a pair, of small size, that stood on each side of the notochord, the pleura-centra, and a crescent shaped piece on the lower side, the intercentrum, that occupies the position of the plate supporting the hæmal arch in the simpler vertebræ. Upon the condition of these four pieces were established the divisions of the suborder *Labyrinthodonta vera.* When the pieces are all separate and in the condition described above, the forms are called rachitomous; the two lateral pieces may fuse and form a ring around the notochord, and at the same time the intercentrum develop from a crescent-shaped piece into a perfect ring, so that each vertebra is represented by two complete rings, this is the embolomerous stage; in the third condition the four pieces fuse to form a solid vertebra; this is most common in the caudal region and may be present there, while in the anterior portion of the column the four original pieces are still separate. This is the stereospondylus condition (Fig. 2).

Another line of development that is quite closely connected with the geological history of the animals is the development of the shoulder girdle. In the more primitive forms, especially the *Branchiosauria* of the Permian, the bones of the shoulder region were largely cartilaginous and were small in size; as we progress through the Carboniferous and into the Triassic time the bones become larger and firmer, until in the latest of the Triassic forms they form a close dermal armor over the underside of the thoracic cavity. In the majority of the forms there is developed in the skin of the abdomen and the lower side of the legs as well, a large number of small bony ossicles that served as a protection for the posterior part of the body. The history of these is also closely connected with the geological progress of the animal; in the earliest forms the ossicles are small and numerous; as the forms progressed the ossicles became larger and less numerous.

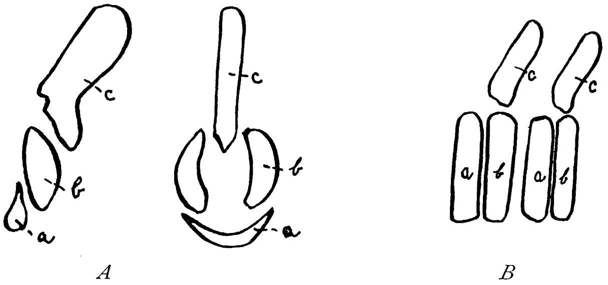

FIG. 2.—*A* Rachitomous vertebra. *B* Embolomerous vertebra. *a* Intercentrum; *b* Pleurocentrum; *c* Neural spine.

BRANCHIOSAURIA.—This is the most primitive group of the *Amphibia*. The forms were all small and salamandriform; there was a short tail, and the limbs were short and weak. The vertebræ in the adult form were barrel-shaped as already described and in the immature form composed of two separate pieces, an upper and a lower. There was no plication of the enamel of the teeth as in the more advanced forms. The bones were largely cartilaginous, the tarsus and carpus and the bones of the occipital portion of the skull entirely so. The ventral surface of the body was protected by a large number of dermal scutes.

Most of these forms are known from the Rothliegende of Germany, but specimens have been found from the same horizon and from the Upper Carboniferous of France and Ohio; from the German region a very large number of forms have been taken in the most excellent state of preservation so that it has been possible to study not only the adult forms, but the young stages as well and to make out the various steps in the metamorphosis of the individual. Credner studied a large series of forms from about 30^{mm} to 120^{mm}, and made out all the stages of development, the growth of the external gills, their loss, and the assumption of the adult form.

Branchiosaurus is the best known genus of the suborder and a description of it may serve as an illustration of the whole group. The head was comparatively large and rounded in front; the edges of both jaws were lined with numerous small, conical teeth; the skull was completely roofed by dermal bones, and the surface of these bones show a very strong sculpture. The condition of the vertebræ, the carpus and tarsus, and the bones of the occipital region was as already described; the limb bones were cartilaginous at the extremities. The eyes were rather large and were protected by bony plates developed in the sclerotic coat, the "sclerotic plates." The whole animal must have presented much the same appearance as one of the modern salamanders and had, probably, much the same habits, never going any great distance from the water.

Melanerpeton, *Apateon*, and *Pelosaurus* from the same locality and horizon as the *Branchiosaurus*, were very similar in appearance, differing only in minor skeletal characters.

Protriton is a form described from the Rothliegende of Autun, in France, and is regarded by some as identical with the early stage of *Branchiosaurus* as it has the external gills and other characters of the larval forms of that genus.

Amphibamus and *Pelion* are from the Carboniferous beds of Ohio. In the first genus the body was rather long; the legs were short with the posterior pair somewhat the largest; the head was rather large and rounded; the teeth were numerous and set close together. *Pelion* had a rather shorter and broader head, the legs were longer and better developed.

MICROSAURIA.—These were in many ways the most highly developed of the *Labyrinthodontia;* the vertebræ, as already explained, approached more nearly the modern type of reptilian vertebræ than any of the group. Their advanced position is evidenced by other parts of the body as well as the vertebræ; all the bones of the body are more perfectly ossified; the bones of the skull are set more firmly together, and the limbs are longer and stronger so that the animal was able to raise the body from the ground, and must have possessed a considerable degree of agility. The carpus and tarsus were ossified, and there were well-developed claws on the feet. Many remains have been found in the trunks and stumps of fossil trees in the working of the quarries in the South Joggins coal region of Nova Scotia, showing that the animals were to some extent at least arboreal in their habits, and that they had reached a freedom of motion and a range of habitat far in advance of that of the other amphibians of the time. It is to this group that we must look, in all probability, for the direct ancestors of the reptiles. The name *Sauromorpha* has been given to the group in recognition of the close relation between it and the *Reptilia.*

Hylonomus and *Hylerpeton* are forms from the South Joggins quarries of Nova Scotia. They were rather elongate in form, with a lizard-like appearance. The vertebræ were well developed, and the whole body was covered with bony scutes instead of the ventral surface only as in most of the forms. The teeth were smooth at the base, but near the top the dentine was somewhat plicated. These were among the best developed of the amphibian forms. It is interesting to note the occurrence of the same genus, *Hylonomus*, in Nova Scotia and in Bohemia.

From the Carboniferous rocks of Ohio, near Linton, have been taken a very large number of the *Microsauria.* Among the most common are *Tuditanus*, *Leptophractus*, *Colosteus*, *Osteocephalus*, and *Ptyonius.*

Tuditanus was rather small form with a short and broad head and the orbits located far forward. There seems to have been a lack of the dermal scutes on the ventral surface and their place was taken by three pectoral shields that exhibit a strong sculpture on the external face; they were the expanded clavicles and the interclavicle. The whole animal was about three to four inches long.

Colosteus reached a length of a foot in some cases. The form was elongate with rather short legs. There were three pectoral plates as in *Tuditanus* as well as a well-developed armor of fine scutes. The teeth were not of equal size, the anterior ones being much the larger.

Ptyonius exhibits a very high degree of specialization. The body was long and serpentiform, and the limbs had entirely disappeared so that the animal had reached the same stage of development as the modern snakes. One very peculiar thing is to be noticed about this form; the distal edges of the transverse processes and neural-spines were fluted or folded so that they present a fan-like appearance.

Leptophractus was by far the largest of the Ohio forms, having about the size of an alligator. Only portions of the skull are known but enough to show that the skull was rather elongate, and that the teeth had the dentine folded as in the true labyrinthodonts. Near the anterior end of the jaw there was a large caniniform tooth.

Osteocephalus resembled in some respects *Ptyonius.* The body was long and snake-like, and the skull was very acuminate. The anterior pair of limbs were absent or rudimentary, and the posterior pair were very short. The three pectoral plates found in most of these forms were absent in this one, and their place was taken by a profusion of slender bony rods that ran obliquely inward and forward covering the whole ventral surface. There were no dermal scutes as in the other forms.

The Carboniferous rocks of Nyran in Bohemia have yielded many forms belonging to the same group, among them are *Hyoplesion*, *Orthacosta*, *Microbrachis*, *Keraterpeton*, and *Urycordylus*.

Hyoplesion is quite similar in structure to *Hylonomus* of the Nova Scotian region, and is regarded by some authorities as synonymous with it.

The other forms do not present any striking peculiarities except *Urycordylus*, which has the same peculiar fluting sculpture of the ends of the transverse processes and the neural-spines as *Ptyonius* and *Osteocephalus* of North America.

AISTOPODA.—This group was very similar in some respects to certain forms of the previous group. The limbs were entirely atrophied as in *Ptyonius;* in addition to this character the parietal and frontal bones were fused into one, and the ribs showed a very peculiar bifurcated condition near the distal end.

Dolichosoma from the Carboniferous rocks of Ireland and Bohemia was quite long, having as many as 150 vertebræ, a number equaled only among the snakes. The skull was small and tapered to a point in front, and there was no evidence of dermal armor.

Ophiderpeton from the Carboniferous of Ireland had a somewhat shorter and broader skull than *Dolichosoma*; the ventral surface of the body was covered with small scutes; the whole animal was about 40–50^{cm} long, and there were in the neighborhood of 100 vertebræ.

Phlegethonia and *Molgophis* are two forms from the same region in Ohio as the *Microsauria* mentioned. They have been considered as synonymous with *Dolichosoma*, which, if true, would indicate a peculiarly wide range for such a specialized form.

LABYRINTHODONTA VERA.—As before stated this group is made up of three subgroups, the *Rachitomi*, the *Embolerimi*, and the *Labyrinthodonti*. The first subgroup is found only in the United States.

RACHITOMI.—In this division, as in the others of the same group, there were many very large forms. The skull was completely covered with thick and heavy membrane bones that showed a deep and intricate sculpture; the whole head was flattened and either very broad in proportion to its length or long and crocodilian in aspect; the base of the skull was in large part cartilaginous; the limbs were short but very strong, and there were five digits on each foot: the tail was of moderate length; the pelvic and pectoral girdles were strong and broad; the pelvis was peculiarly like that of the modern frog in many of the forms; the vertebræ were made of several distinct pieces as already described. The known forms of the group are almost entirely from the Permian rocks of Europe, the East Indies, and North America.

Archægosaurus from the Rothliegende of Germany was rather crocodilian in aspect; the head was long and slender and joined to a rather elongate body. In youth the animal was furnished with external gills as in the modern salamanders, which were probably shed when the animal reached maturity; the dentine of the teeth was arranged in a radial manner the first step towards the intricate folding of the enamel in the more advanced forms; the clavicles and the interclavicle were broad and strong covering to some extent the lower surface of the thorax.

Chelydosaurus from the Rothliegende of Bohemia was shorter than *Archægosaurus* with a broad head and large orbits; the dermal bones covering the head were sculptured in a peculiar radial fashion. Nearly every portion of the skeleton is known, and the preserved bones show that the animal was rather in advance of the majority of the forms of the time as they are almost entirely free from cartilage.

Discosaurus is a closely related form from the same horizon in the neighborhood of Dresden.

Actinodon and *Euchirosaurus* are from the lower Permian (Rothliegende) of France. The first was much like *Archægosaurus*, but the head was shorter and more triangular in outline; the length of the skull was about 18^{cm}. The second genus is less well known than the first, but is remarkable for the strength and perfection of the limb bones, especially the articular surfaces which, as a general thing, are not well developed even in the recent amphibians.

Melosaurus from the Keupfer sandstone of Orenbourg in Russia was, so far as the imperfect specimen can be interpreted, quite similar to *Archægosaurus;* it has been suggested that it may be the same genus; if this is true, it would indicate a very wide range of distribution for the animal.

Trimerorachis and *Eryops* are from the Permian deposits of Texas in the United States. Only the lower division of the Permian, the Wichita division of the Texas geologists, has yielded any vertebrate fossils, but in this horizon there is a somewhat abundant fauna of amphibians, reptiles and fishes. In the neighborhood of Danville, in eastern Illinois, there have been found remains of the same amphibians that are found in the Texas deposits; the area is only a small one and is regarded as the course of an old river that has cut its bed through the underlying Carboniferous rocks. Some fragments of the same animals have been found in New Mexico. Of the genus, *Eryops*, Cope, the describer says, "this is the largest of American batrachians, the skull measuring a foot wide by eighteen inches long. It was very abundant constituting with the reptilian genus, *Dimetrodon*, the most prominent type of the Permian fauna in this country. The vertebral column is slender when compared with the size of the limbs and especially the head." Of the genus *Trimerorachis* he says, "the head of *T. insignis* is wide, flat and rounded, and its superior surface is strongly wrinkled. The lyriform mucous grooves do not extend behind the orbits. This was an abundant species during the Permian time in Texas, and probably possessed aquatic habits."

Acheloma and *Anisodexis* are forms from the Permian of Texas that are less well known than the foregoing and are perhaps synonymous with *Eryops*.

EMBOLERIMI.—These are perhaps the most interesting of the *Layrinthodontia*; as already indicated they are distinguished by the fact that the vertebræ are made up of two rings formed by the upward growth of the lower segment of the vertebra of the rachitomous type and the downward growth of the upper segment and its union with the two lateral segments.

Cricotus, the best known form is from the Permian deposits of Texas, the same locality as the rachitomous forms. It was rather long and crocodilian in aspect and the head was covered with the same kind of membrane plates as in the other genera but they were devoid of sculpture; the orbits were large and placed far forwards.

Diplovertebron from the Gaskohle of Bohemia is known only from fragments of the skull, limb bones and vertebræ, but the vertebræ show the same structure as *Cricotus*.

LABYRINTHODONTI (STEREOSPONDYLI).—These are the very large form that appeared at the end of the Palæozoic and reached their greatest development during the Triassic. They possessed complete biconcave vertebræ with a central foramen for the passage of the notochord. The most peculiar feature of the group, is the arrangement of the outer layer of the teeth; instead of the usual smooth layer the enamel is thrown into the most complicated folds so that a cross section of the tooth has an almost dendritic appearance. In other features than the teeth the group evinces its advanced position among the amphibians; the bones of the skull are all well ossified and the base of the skull is composed entirely of bone instead of being partly cartilaginous as in the preceding groups; there is no trace of the grooves on the upper surface of the skull to mark the position of the sensory tracts; the thoracic region is completely protected by the development of the clavicles and the interclavicle into large and strong plates that are tightly joined together; the posterior abdominal region is also protected by the expansion of the bones of the pelvis though not to the extent reached in the anterior girdle; the limb bones are all well ossified and the carpus and tarsus were entirely bony; the feet were provided with strong claws.

Trematosaurus from the Buntersandstein, near Bernberg, in Germany, was one of the smaller forms; the skull was about

24^{cm} long and rather narrow, giving the skull a rather crocodilian appearance; the edges of the maxillaries were lined with small, nearly equal sized teeth that were opposed to a similar series on the lower jaw; besides the rows of teeth on the maxillaries there were a number of larger teeth on the palatines and the vomer, covering the roof of the mouth with a strong dentition.

Metoposaurus (*Metopias*) from the Keupfer sandstone of Germany was nearly twice as large as *Trematosaurus*, the skull measuring about half a meter. The shape of the skull was much the same as in *Eryops* of the American Permian, being broad and stout, depressed from above downwards and showing a decided sculpture on the outer surface of the bones; the genus is peculiar for the very strong development of the pectoral shields, the interclavicle is a broad, diamond-shaped bone on either side of which are joined the clavicles that are also developed into broad plates, the whole covering the ventral side of the anterior portion of the body; all three of the bones exhibit a rugose outer surface.

Capitosaurus from the same locality and horizon as *Trematosaurus* was nearly as large as *Metoposaurus;* the orbits were small and elliptical; the nares large and located far forward; the extremity of the snout was broad and blunt. The same dentition is found in this as in the previous form, a series of small teeth on the edges of the upper and lower jaws and a few large tusk-like teeth on the palatines and the vomer; the surface of the skull shows a slight trace of the sensory canals and the bones are deeply pitted with grooves radiating outward to the edges of the bone.

Mastodonsaurus from the Lettenkohl, the lower division of the Keupfer, reached the largest size of any of the *Labyrinthodonti;* the skull in some specimens reaching a meter in length. The skull was rather triangular in outline; the eyes were small and the nares located far forwards; the grooves marking the course of the sensory tracts are very distinct; there was a double instead of a single row of small teeth on the edges of the upper and the lower jaws and there were two or more enlarged palato-vomerine tusks on each side. The whole animal had a probable length of about ten feet, the head being disproportionately large.

Labyrinthodon from the same horizon as the previous forms is, according to Lydekker, a synonym of *Mastodonsaurus*. It was described by Owen from a single tooth and the name was founded on the peculiar folding of the dentine. As most all of the *Labyrinthodonti* have the same character the distinction fails; it is as well however to know the genus as the name is a common one in the text-books. (See Owens, *Odontography*, Pl. LXIII. Fig. 1, for a picture of the structure of the labyrinthodont tooth.)

Nyrania from the Permian of Bohemia and *Bothriceps* and *Micropholis* from the Permian of South Africa are less well known foreign genera. Certain imperfectly preserved remains have been collected from the rocks of the Newark system of Pennsylvania and North Carolina. *Eupelor* is the name of the small form from Pennsylvania, and *Pariosteigus* and *Dictyocephalus* from the Carolina region. Quite recently a tooth has been described from the Upper Carboniferous of Kansas, and referred to the genus *Mastodonsaurus;* if the determination is correct this indicates a rather peculiar distribution for the genus as it is unknown from the English deposits, though quite common on the continent.

Below is a summarized list of the most important forms of the *Labyrinthodontia* with their geological range and habitat so far as known.

LABYRINTHODONTIA.
- *Branchiosauria.*
  - *Branchiosaurus*, Rothliegende, Germany.
  - *Melanerpeton*, *Apateon* and *Pelosaurus*, Rothliegende, Germany.
  - *Protriton*, Rothliegende, France.
  - *Amphibamus* and *Pelion*, Carboniferous, Ohio.
- *Microsauria.*
  - *Hylonomus* and *Hylerpeton*, Carboniferous, Nova Scotia.
  - *Tuditanus*, *Osteocephalus* and *Colosteus*, Carboniferous, Ohio.
  - *Hyoplesion* and *Microbrachis*, Carboniferous, Bohemia.
  - *Lepterpeton* and *Keraterpeton*, Carboniferous, Ireland.

- *Dolichosoma* and *Ophiderpeton*, Carboniferous, Ireland.
- *Molgophis?* and *Phlegethonia?*, Carboniferous, Ohio.

Labyrinthodonta vera.

- *Rachitomi.*
  - *Archægosaurus*, Rothliegende, Germany.
  - *Chelydosaurus*, Rothliegende, Bohemia.
  - *Actinodon* and *Euchirosaurus*, Rothliegende, France.
  - *Trimerorachis* and *Eryops*, Permian, Texas.
- *Embolerimi.*
  - *Cricotus*, Permian, Texas.
  - *Diplovertebron*, Permian, Gaskohle, Bohemia.
- *Labyrinthodonti.*
  - *Trematosaurus*, Buntersandstein, Germany.
  - *Metoposaurus*, Keupfer, Germany.
  - *Capitosaurus*, Buntersandstein, Germany.
  - *Mastodonsaurus*, Keupfer, Germany.
  - *Micropholis* and *Bothriceps*, Permian, South Africa.
  - *Eupelor*, *Pariosteigus*, and *Dictyocephalus*, Triassic, Pennsylvania, and North Carolina.

Besides the remains of fossil forms the rocks of the Carboniferous and Triassic times have yielded a large number of tracks, made when the animal walked across some mud flat. These tracks have received the name of *Ichnites*. Such tracks in the Carboniferous rocks are known from Kansas and Nova Scotia. Most of the tracks however occur in the Triassic rocks; the red sandstone of the Connecticut River Valley has yielded a large number. Prominent among them is the form described as *Brontozoum*. These are enormous tracks, the middle digit having a length of 12.5 inches and the whole foot 14 to 18 inches. The whole animal must have been twelve to fourteen feet long.

Anisopus from the same locality had the hind foot nearly twice as large as the front foot.

Anomœpus had five digits on the front foot and only three on the hind foot. (This form may very possibly have been reptilian).

Chierotherium or *Chierosaurus* from the Buntersandstein of Europe was about half the size of *Brontozoum*, The hind foot was about twice the size of the front foot, and there were five digits on both. The same form is known from the Triass of Cheshire in England.

It is altogether probable that many of these tracks belong to forms already described from parts of the skeleton but until some one shall be so fortunate as to discover the skeleton and the tracks together it will be impossible to detect the synonymy. It has been suggested that the tracks referred to as *Cheirosaurus* belong either to *Capitosaurus* or to *Trematosaurus*.

The whole of the order *Labyrithodontia* dies out in the Triassic but the degree of specialization to which the members of the order attained bears ample witness to the important part they played in the fauna of the Carboniferous and the first part of the Mesozoic. Only by the demands of a most severe struggle for existence could there have arisen within the limits of a single order the necessity for the great divergence of forms that we find among the *Labyrinthodontia*. The wide distribution of the forms also bears witness to their prominence, forms being known from the East Indies, South Africa, Europe, England, and North America.

The remaining orders of the amphibians are unknown before the Cretaceous.

The *Caudata* (*Urodela*) are lizard-like, tailed animals with a naked skin and with or without persistent external gills. The skull lacks certain of the bones found in the posterior part of the skull of the *Labyrinthodontia*, as the supratemporal, supraoccipital, and the postorbital. The vertebræ are complete in a single piece. There are two suborders of the *Caudata*, the *Ichthyoidea*, in which the vertebræ are biconcave, and the *Salamandrina*, in which they are opisthocoelus or concave behind and convex in front. The common *Siren*, *Proteus*, and *Menobranchus* are living representatives of this order. Among the fossil forms perhaps the most interesting is the *Andrias* from the fresh water Miocene of Œningen. This form was described as early as 1726 by Scheuchzer, who considered the imperfect skeleton which he had as the remains of an antediluvian man, and gave to it the name "homo diluvii testis et theoscopos." The same form was afterwards described as fish and as a lizard, until finally its true nature was made out. The form reached a length of about four feet in the largest specimens and was one of the largest of the *Caudata*. In most of its skeletal characters it was very similar to the modern *Menobranchus*.

Megalotriton is one of the *Salamandrina* from the Upper Eocene of France. It was of considerable size, judging from the vertebræ and the detached bones of the limbs. No complete skeleton has been found.

The *Anura* (*Ecaudata*) are little known from the fossil forms. They appear in the Tertiary with almost as many genera and species as at the present time, and there has been little change in the forms.

The origin of the modern forms of the amphibians is not known. Zittel says of these forms that they can in no sense be derived from the labyrinthodonts, for between these and the modern forms there exists not only a great morphological gap, but a great break in the geological record as well.

III. REPTILIA.

PAREIASAURIA.—The simplest of the *Reptilia* differ very little from the *Amphibia*. There is little in the structure of the *Pareiasauria* that might not belong to the *Labyrinthodontia* except the arrangement of the bones forming the base of the skull. Add to this that the animal did not undergo a metamorphosis from a water to a land form and the list of differences is complete. All during the Carboniferous time the conditions had been growing better and better fitted for the existence of purely terrestrial, air-breathing forms, and at the end of that time, if not, as there is reason to think, some time before, there appeared the forerunners of the great tribe of reptiles. As has been indicated, the *Microsauria* were in all probability the direct ancestors of the reptiles, but the evidence of the preserved forms is so incomplete that we do not have either what must have been the last step of the amphibian line or the first of the reptilian. The development of reptilian forms at the beginning and throughout the Permian time was most remarkable; it seems as if the conditions had been preparing for a long time and with the dawn of the Permian disappeared the last obstruction to the growth of the reptiles which appeared at once in the greatest profusion. Not only were there great numbers of forms, but they were, even in the earliest time that we know them, already highly specialized. The group that is discussed first, the *Pareiasauria*, is nearest to the amphibia in many of its characters, while in others it is one of the most specialized of all the vertebrates. The Permian time has perhaps a larger number of highly and curiously specialized forms than any other time.

In 1840 there was discovered in the Karro formation, Permian or Permo-Triassic, of South Africa, a large number of fossil remains that were shipped to the British Museum, and there described by Professor Owen as a reptile closely related to the dinosaurs, and named by him, *Pareiasaurus bainii.* Later a nearly perfect skeleton was found and described by Professor Seeley, who redescribed the genus and species and placed it in a distinct order, the *Pareiasauria* (1863). As this animal is typical of the whole group it may be described somewhat in detail.

Pareiasaurus was one of the largest as well as one of the most amphibian-like of all the reptiles. The head was covered with large bony plates that had practically the same arrangement as in the *Labyrinthodontia;* the bones formed a complete roof, leaving only five openings in the skull, the orbits, nares, and the pineal foramen; there were traces of the sensory tracts on the surface of the skull, as in the largest of the *Labyrinthodonti;* the teeth were equal in size and distributed all around the edges of both jaws in an even series; there were small teeth arranged in rows on the palatine and the vomer bones in the roof of the mouth; the limbs were short and strong, with well-developed articular surfaces, and the feet were provided with strong claws; there were eighteen presacral vertebræ. This is of considerable interest, as the number is the same that occurs in the turtles, and this is one of the few clues that we have as to the origin of the turtles. The vertebræ were biconcave, but were not perforated for the passage of the notochord, which was consequently divided into intervertebral segments. In the skin of the back directly over the spinal column there were developed three rows of bony ossicles, the middle row lying directly over the spinous processes and the other two lying upon each side; this development of dermal plates is regarded as the first step toward the formation of a carapace, and as an additional evidence of the connection of the *Pareiasauria* with the turtles. The thoracic girdle is stout and heavy and retains the central element, the interclavicle, which is lost in the majority of the reptiles; the pelvis was large and massive. In life the animal must have presented the appearance of a large amphibian; the legs were too short to lift the body off the ground, so the belly must have dragged as in the crocodiles; the whole body was short and squat and the tail was short; the skin was without scales and was probably thickened and folded.

Scattered bones indicate the presence of at least two other genera, *Propappus* and *Anthodus*, in the South African deposits, but not enough of the skeleton is known to warrant a description. In the American Permian deposits of Texas and Illinois there have been found a large number of forms belonging to this order; the best known are *Diadectes*, *Empedias*, *Chilonyx*, *Pantylus*, and *Pariotichus*.

Diadectes and *Empedias* are the best known of the forms; they are similar to *Pareiasaurus*, though they did not reach the size of that form; they had the same broad, flat skull with few openings; the teeth are different from the African form, in that, although they are similar in size and arranged in regular order around the edges, they are not simple in form, but are expanded laterally so that they exhibit broad grinding surfaces instead of cutting edges; they were undoubtedly herbivorous forms; the number of the presacral vertebræ is unknown, but it was probably greater than in *Pareiasaurus;* the vertebræ were greatly flattened in the antero-posterior direction and expanded laterally; this feature, with the short and stout limbs, led Cope to suggest that they were possibly fossorial in habit.

The three remaining forms mentioned have been placed in a separate family from the preceding, the *Pariotichidæ;* they are all smaller than *Diadectes*, never exceeding a length of two or three feet, and are further distinguished by the fact that the teeth are not equal in size in all parts of the jaw, the teeth of the middle part of the maxillary series being larger than the others. Certain of the less well known of the Texas forms show broad bony plates that extend outward from the middle of the back and cover the ribs to a large extent; they correspond to the ribs in number and position. This is a very close approximation to the condition in the turtles; in *Otocœlus* the plates are especially well developed and the lateral edges of adjacent plates meet.

The taxonomy of this group and its related forms is very imperfectly understood and there has resulted little but confusion from the numerous schemes of classification that have been proposed. When the first of the African fossils were discovered and described the name *Anomodontia* was proposed by Owen for the whole series of African forms, as he supposed that they were all closely related, but he soon recognized that this was not true and separated a group, the *Theriodontia*, to include the forms with a more carnivorous dentition. Later writers have found it necessary to depart very widely from this scheme and have founded new orders and in some cases done away with the original ones. Out of this tangle one thing seems very clear, the order *Pareiasauria* is a distinct order separate from all the rest of the Permian reptiles and is the primitive form of all the reptiles. Other forms that are closely related to this order, but whose structure is too incompletely known to make the determination of their position definite, had best here be retained in the original order *Anomodontia* as suggested by Seeley and Lydekker. The classification of the forms will then stand as follows :

Order *Pareiasauria.*
  Fam. *Pareiasauridae* (African forms).
    Diadectidae (American forms).
    Pariotichidae (American forms).
    Elginidae (European forms).[1]
Order *Anomodontia.*
  Suborder *Dicynodontia.*
    Placodontia.
    Theriodontia.

The *Dicynodontia*, including the genera *Dicynodon*, *Oudenodon*, and *Ptychosiagum* (*Ptychognathus*), are all from the same locality, South Africa, as *Pareiasaurus*, and from the same geological horizon.

Dicynodon is known only from the skull and is one of the most peculiar of the reptilian forms; the jaws were edentulous except for the presence of two large tusk-like teeth that grew out from the anterior part of the upper jaw just in the position occupied by the canine teeth in the mammals; the part of the upper jaw anterior to these teeth and the lower jaw were protected by a horny sheet similar to that present in the turtles; the posterior part of the skull was perforated by large fossae that served to lighten it considerably. This process of lightening the skull by the development of large fossae in the posterior, temporal portion, is a constant feature of all the reptiles above the *Pareiasauria* with the exception of the turtles. Many scattered bones have been found in the same deposits as the skulls of *Dicynodon* that may belong to the same genus, but there is not sufficient evidence to say definitely that this is true, and until the vertebral column and the limb bones are made out it will be impossible to determine accurately their position with relation to the other reptiles.

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[1] *Elginia* is an imperfectly known form from the Elgin (Triassic) sandstones of Scotland. There are no bones preserved, but only the impression of the bones in the soft sandstone from which all the bony tissue has rotted out. The fossils were studied from casts made of the cavities left by the decayed bones. The animal was of considerable size, nearly as large as *Pareiasaurus* and the teeth were arranged in a regular series around the edges of the jaws; the appearance of the skull in life must have been most peculiar, the presence of strong rugosities on the surface of the bones of the skull show that the head was covered with large horns. *Geikia* was a related form from the same locality and horizon.

Oudenodon was also described from the skull alone; the jaws are entirely edentulous and the appearance of the skull is strikingly testudinate. It has been suggested that this is the female of *Dicynodon*.

Ptychosiagum, or as it is more generally known, *Ptychognathus*, was very similar in many respects to the *Dicynodon*, having the same horny covering to the anterior portion of the jaws and the large canine teeth in the upper jaw; the peculiar part about the animal was the bending of the facial portion at almost a right angle to the upper surface of the skull and the upward extension of the anterior end of the lower jaw so that the mouth seemed to open on the superior face of the skull.

All of these animals must have been herbivorous; the large canine teeth were probably used to tear up the roots and aquatic plants upon which they fed. They could have been of no use as organs of offense or defense.

Placodontia.—These are rather problematical forms from the Muschelkalk (Triassic) of Germany. As in the case of the *Dicynodontia* the bones are all isolated and the various genera are known from the skulls; the few other bones that have been found in the same deposits may or may not belong with the skulls. Lydekker has called attention to the fact that all the bones that are found with the skulls are either dinosaurian or plesiosaurian; if it should turn out that the plesiosaurian bones belong with the skulls of the Placodontia it may be that that group belongs very far from the *Anomodontia* with which they are here placed, but until that is established it is perhaps best to take the evidence of the skull which points to a very decided relationship between the two groups. *Placodus* and *Cyamodus* are the two described genera.

Placodus was first described by Agassiz from a single tooth, and was regarded by him as a fish. The error was not corrected until the entire skull of the form was known. The skull was triangular in outline, very broad behind and rapidly narrowing to a pointed rostrum in front; the orbits were large and the anterior nares very small; the posterior part of the skull shows the presence of the fossae already mentioned. The teeth are the most striking features of the skull, the anterior incisors were chisel-like and prehensile; the maxillaries were broad and flat; there were five on each side; besides the maxillary teeth there were three large palatine teeth on each side, so large that they covered nearly the whole roof of the mouth. The broad, low teeth of both this and the succeeding forms seem to indicate that the animals were accustomed to a molluscan diet.

Cyamodus was very similar to *Placodus*, but there were no prehensile incisor teeth and there were five palatine teeth, the posterior pair far exceeding the anterior ones in size.

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